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Plant property regulates soil bacterial community structure under altered precipitation regimes in a semi-arid desert grassland, China

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Abstract: Variations of precipitation have great impacts on soil carbon cycle and decomposition of soil organic matter. Soil bacteria are crucial participants in regulating these ecological processes and vulnerable to altered precipitation. Studying the impacts of altered precipitation on soil bacterial community structure can provide a novel insight into the potential impacts of altered precipitation on soil carbon cycle and carbon storage of grassland. Therefore, soil bacterial community structure under a precipitation manipulation experiment was researched in a semi-arid desert grassland in Chinese Loess Plateau. Five precipitation levels, i.e., control, reduced and increased precipitation by 40% and 20%, respectively (referred here as CK, DP40, DP20, IP40, and IP20) were set. The results showed that soil bacterial alpha diversity and rare bacteria significantly changed with altered precipitation, but the dominant bacteria and soil bacterial beta diversity did not change, which may be ascribed to the ecological strategy of soil bacteria. The linear discriminate analysis (LDA) effect size (LEfSe) method found that major response patterns of soil bacteria to altered precipitation were resource-limited and drought-tolerant populations. In addition, increasing precipitation greatly promoted inter-species competition, while decreasing precipitation highly facilitated inter-species cooperation. These changes in species interaction can promote different distribution ratios of bacterial populations under different precipitation conditions. In structural equation model (SEM) analysis, with changes in precipitation, plant growth characteristics were found to be drivers of soil bacterial community composition, while soil properties were not. In conclusion, our results indicated that in desert grassland ecosystem, the sensitive of soil rare bacteria to altered precipitation was stronger than that of dominant taxa, which may be related to the ecological strategy of bacteria, species interaction, and precipitation-induced variations of plant growth characteristics.

Keywords: plant-microbe interactions; bacterial community diversity; bacterial community composition; bacterial interactions; precipitation gradients

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1 Introduction

Global warming affects the hydrological cycle around the world, resulting in shifts in precipitation regimes, such as increased inter-annual precipitation variability and frequent

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extreme precipitation events (IPCC, 2013; Prein et al., 2017). The arid and semi-arid regions are usually characterized by low precipitation and limited nutrients (Makhalanyane et al., 2015), which are highly sensitive to altered precipitation. Variations of precipitation have great impacts on soil carbon cycle and decomposition of soil organic matter in semi-arid grassland (Fierer and Schimel, 2002; Knapp et al., 2002). Soil microorganisms are crucial participants in regulating these ecosystem processes (Standing et al., 2005; Zhang et al., 2013) and vulnerable to the changes in abiotic and biotic factors caused by altered precipitation (Chen et al., 2019; Na et al., 2019; Jordan et al., 2020; Yang et al., 2021). Therefore, changes in soil microbes caused by altered precipitation can affect soil carbon cycle and regulate soil carbon storage through decomposition of soil organic carbon and heterotrophic respiration (Standing et al., 2005; Zhang et al., 2013). Investigating how changes in precipitation influence soil microbial community structure is vital for understanding the potential impacts of altered precipitation on soil carbon cycle and carbon storage.

Soil bacteria are more sensitive to altered precipitation than soil fungi (Yang et al., 2021), because bacterial movement and substrate diffusion are limited by the changes in soil water resulted from altered precipitation (Harris, 1981). In addition, bacteria make up the largest proportion of soil microorganisms (Zhang et al., 2005). Most studies have found that dominant soil bacterial phyla in grassland ecosystems included Actinobacteria, Acidobacteria, and Proteobacteria under altered precipitation (Zhao et al., 2017; Ochoa-Hueso et al., 2018; Wu et al., 2020; Wang et al., 2021). The sensitivities of soil dominant bacteria and low abundant bacteria to altered precipitation are different. Several researchers found that altered precipitation significantly affected the relative abundance of dominant bacterial phyla (Ochoa-Hueso et al., 2018; Chen et al., 2019). However, other researchers found that only the relative abundance of rare bacterial phyla was significantly affected by altered precipitation (Zhao et al., 2017; Wu et al., 2020). Furthermore, the response patterns of soil bacteria to altered precipitation depend on their ecological strategies (Lennon et al., 2012). For example, precipitation addition treatments usually increased the relative abundance of copiotrophic taxa (Meier and Bowman, 2008). This is because soil nutrient availability improves as soil moisture and nutrients input increase under increased precipitation treatments (Meier and Bowman, 2008). Proteobacteria, a member of copiotrophic taxa, was found to be more abundant when precipitation increased in a semi-arid grassland (Chen et al., 2019), temperate desert (Huang et al., 2018), and meadow steppe (Yang et al., 2021). However, the relative abundance of Proteobacteria maintained changeless under altered precipitation in the subtropical forest (Zhao et al., 2017). Therefore, these inconsistent results about the response patterns of soil bacterial community composition to altered precipitation may be related to the ecosystem-specific background, soil bacterial survival strategies or their adaptability to altered precipitation.

In addition, high-throughput sequencing technology can provide insight into the response patterns of soil microbial diversity to altered precipitation. For example, in the desert steppe, an increase in precipitation leads to an improvement in soil moisture conditions, thereby promoting the increase of soil bacterial diversity (Sorensen et al., 2013; Wang et al., 2021). Conversely, a reduction of precipitation can decrease soil bacterial diversity (Yang et al., 2021). However, some studies conducted in the desert steppe found that soil bacterial diversity did not significantly change with altered precipitation (Na et al., 2019; Li et al., 2022). This was related to the survival strategies of soil microorganisms in response to altered precipitation. For example, in soil with a history of drought, soil bacterial diversity was found to increase under drought treatment (Preece et al., 2019). This further confirmed that the survival strategies of soil bacteria can drive the changes in bacterial diversity under altered precipitation. These inconsistent results about precipitation-induced effects on bacterial communities may be attributed to the ecosystem-specific background, history precipitation regimes or bacterial survival strategies in response to altered precipitation (She et al., 2018).

Variations of precipitation significantly affected soil microbial community diversity and composition via changing plant growth characteristics and soil physical-chemical properties (Na et al., 2019; Yang et al., 2021). First, the changes in plant species can promote environmental heterogeneity by affecting the quantity and quality of plant residual (e.g., root exudates and litter) and nutrient availability, thereby resulting in the variations of soil microbial communities

(Boeddinghaus et al., 2019). For example, Chen et al. (2017) and Li et al. (2017) found that plant diversity was an important driver of soil bacterial community. However, another study showed that there were no significant changes in bacterial community structure and diversity as plant diversity increased (Kuramae et al., 2011). Plant aboveground biomass, as major resource inputs to soil (De Deyn et al., 2008; Liu et al., 2021), was regarded as a contributor of the bacterial community composition in the SEM (structural equation model) analysis (Na et al., 2019). Second, altered precipitation can regulate the bacterial communities by directly affecting soil physical-chemical properties, such as soil water content (SWC), total phosphorus (TP), soil organic carbon (SOC), and pH (Na et al., 2019; Yang et al., 2021; Li et al., 2022). Broadly speaking, the positive effect of increased precipitation on soil water availability can provide more nutrients and promote their accessibility (Manzoni et al., 2012; Manzoni et al., 2014). This increase in nutrient availability can promote the growth of copiotrophic groups and enhance bacterial diversity (Chaudhry et al., 2012). Most studies in a meadow steppe (Yang et al., 2021) and the Junggar Basin (Wu et al., 2020) found that the improvement of SWC caused by increased precipitation treatments changed soil bacterial diversity. However, SWC did not drive the changes in soil bacterial community diversity and composition in subtropical forest (Zhao et al., 2017) and the degraded shrub- and grass-dominated community (Umair et al., 2020). Few studies focus on the contributing factors of altered precipitation on soil bacterial communities in these fragile ecosystems of Northwest China (Jia et al., 2017). Therefore, the in-depth knowledge of influencing mechanism of altered precipitation on soil bacterial community is helpful to predict the feedback effects of climate changes on soil carbon cycle and storage in desert grassland.

To study the potential impacts of altered precipitation on soil bacterial communities in desert grassland in the northwestern Chinese Loess Plateau, we conducted a field manipulated experiment by setting five precipitation gradients. Our hypotheses are as follows: (1) precipitation changes can significantly affect soil bacterial community diversity and composition; and (2) precipitation changes can significantly affect the diversity and composition of soil bacterial community via mediating plant and soil properties.

2 Materials and methods

2.1 Study area

This study was carried out at the Gaolan Experiment Station for Ecology and Agriculture Research (36°13″N, 103°47″E; 1780 m a.s.l.), Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, located in the northwestern Chinese Loess Plateau. The climate is drought-prone, semi-arid, and continental. The mean annual precipitation is 263 mm, and most of precipitation events occur in the summer season (May–September). The annual mean temperature is 8.4°C, with the minimum monthly mean temperature of −9.1°C (January) and the maximum monthly mean temperature of 20.7°C (July) (Zhang et al., 2018). The mean annual evaporation is 1786.0 mm. The average SOC and total nitrogen (TN) are 0.8% and 0.1%, respectively, and soil pH is 8.5 (Zhang et al., 2018). According to the soil classification system, the soil is mainly categorized as Haplic Calcisol, which is developed from wind-accumulated loess parent material, and is characterized by uniform silt loam texture (Zhang et al., 2018). The area is mainly covered with typical desert steppe vegetation, which is predominated by *Ajania fruticulosa* (Ledeb.) Poljak (Compositae) and *Stipa breviflora* Griseb. (Gramineae). Accompanying species were *Peganum harmala* L. (Zygophyllaceae), *Zygophyllum mucronatum* Maxim. (Zygophyllaceae), *Artemisia capillaris* Thunb. (Compositae), *Cleistogenes squarrosa* (Trin.) Keng (Gramineae), and *Salsola ruthenica* Iljin (Chenopodiaceae).

2.2 Experimental design

According to the variation of precipitation in the study area in the past 50 a (from −41% to +40%), the experiment conducted a randomized complete block design with five precipitation gradients: −40% and −20% of natural growing season precipitation (DP40 and DP20), natural growing season precipitation as a control (CK), and +20% and +40% of natural growing season precipitation (IP20 and IP40). Precipitation timing and frequency were constant in the experimental site. Three replicated plots (2.5 m×2.5 m) were established for each treatment in an

area of relatively homogeneous grassland. The precipitation manipulation experiments were conducted from May to September in 2013, 2014, and 2015.

The rainout shelters were used to reduce 20% and 40% of natural growing season precipitation for the drought treatments (DP20 and DP40), respectively. The shelters consisted of a steel frame with transparent acrylic bands (V-shaped, 10 cm wide) covering 20% and 40% of experimental plots above it (Zhang et al., 2018). The average height of the shelter was 0.5 m. The shelter had gutters on its lower side in order to channel the intercepted water to an enclosed container. Compared with plastic or poly vinyl chloride (PVC), acrylic has higher light transmittance and intercepts lower photosynthetic active radiation. The secondary micro-environmental effects can be minimized by opening shelter sides, such as maximizing air motion, minimizing differences in temperature, and relative humidity artifacts. Rainwater intercepted by the roof bands in decreased precipitation treatments (collected by gutters) was applied to the corresponding increased precipitation treatment plots (IP20 and IP40) manually within 8 h of each precipitation event.

2.3 Plant community investigation

Plant species composition was recorded in one subplot (1 m×1 m) at the center of each plot. Plant species richness, the density of each species, coverage, and height were measured monthly from late May to late September in 2019. Species richness was calculated from the number of plant species in subplots. Plant density was the sum of individual numbers of each species. Coverage was estimated from a frame (1 m×1 m) with 100 equally distributed grids. The species height was the average value of individual plant heights.

Aboveground biomass (AGB) was estimated using harvesting method at the time of peak biomass (early September) in 2019. All plants were clipped to the soil surface by species in another two random subplots (0.5 m×0.5 m) in each plot. The biomass (g/m^2) of each species was dried in an oven at 65°C for 48 h. The sum AGB of all species was used to estimate the community AGB (g/m^2).

Plant community diversity was calculated through Shannon's index (H'):

$$H' = -\sum_{i=1}^{s} P_i \ln P_i, \quad (1)$$

where H' is the Shannon's index; P_i is the proportion of the individual number for i^{th} species to the total number of plants in a community; and S is the encountered species number.

2.4 Soil sampling and property analysis

In August 2019, we collected three soil samples with a soil auger (5 cm in diameter, 0–10 cm in depth) along the diagonal (both ends and midpoint), and then mixed them as a single sample in each plot. All soil samples were placed in an icebox and taken back into the laboratory. After soil was immediately mixed and sieved at 2 mm, half of each composite sample was air-dried for soil physical and chemical property analysis. The other half was used for deoxyribonucleic acid (DNA) isolation (stored at −80°C) and microbial biomass carbon (MBC).

SWC was determined by using oven-drying method. MBC was measured through fumigation-extraction method (Brookes et al., 1985). Soil TP, TN, and SOC contents were detected by a UT-1810PC spectrophotometer (Persee, Beijing, China), Kjeldahl digestion, and $K_2Cr_2O_7$-H_2SO_4 oxidation method, respectively (Bao, 2000). Soil available phosphorus (SAP) was measured by Bray method (Bao, 2000). Soil available nitrogen (SAN) was measured by a flow analyzer (Skalar 8505, Skalar Analytical BV, Breda, the Netherlands). Soil available potassium (SAK) was determined by ammonium acetate extraction and flame spectrophotometry (Bao, 2000). Additionally, soil pH was determined by a glass electrode with a soil:water ratio of 1.0:2.5 (Bao, 2000). The electrical conductivity (EC) was determined by an EC meter with a soil:water ratio of 1.0:2.5 (Bao, 2000).

2.5 Analysis of soil microbial community

We extracted microbiome genomic DNA from replicate samples (n=3) using MP FastDNA SPIN Kit (MP Biomedicals Co., Ltd., Shanghai, China) for soil according to the manufacturer's instructions. The concentration and purification of DNA extracts were determined using

NanoDrop 2000 UV-vis spectrophotometer (Thermo Scientific, Wilmington, USA). The hyper variable region V3-V4 of bacterial 16S rRNA (ribosomal ribonucleic acid) gene was amplified using 338F/806R primers to estimate soil bacterial community diversity and composition in each sample. Based on previously described scheme (Caporaso et al., 2011), we performed PCR (polymerase chain reaction) amplification of 16S rRNA gene. High-throughput sequencing of amplicons was conducted through the Illumina MiSeq platform at Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China). The mean sequencing depth of individual samples in 2019 were 43,705 clean reads (from 32,794 to 54,938). The complete bacterial datasets for this study have been uploaded to the National Center for Biotechnology Information (NCBI) Short Read Archive (SRA) database with accession number SRP405290.

Paired reads from the original DNA fragments were merged by FLASH v.1.2.7 (Magoč and Salzberg, 2011). In each sample, we performed the assignment of sequencing reads based on different individual barcodes. Sequences were analyzed using QIIME (quantitative insights into microbial ecology) software package (Caporaso et al., 2010) and UPARSE v.7.1 (Edgar, 2013). Operational taxonomic units (OTUs) were filtered with 97% similarity (Edgar, 2013). The taxonomy of each OTU representative sequence was analyzed through RDP (ribosomal database project) Classifier v.2.2 (Wang et al., 2007) against 16S rRNA database using a confidence threshold of 0.7.

2.6 Statistical analysis

One-way analysis of variance (ANOVA) followed by least significant difference (LSD) test was used to detect the differences in plant growth characteristics (plant species richness, Shannon's index, coverage, density, height, and AGB), soil physical-chemical properties (SWC, MBC, SOC, TN, TP, SAN, SAP, SAK, pH, and EC) and bacterial community diversity among different precipitation treatments. The LEfSe (linear discriminate analysis (LDA) effect size) method was used to analyze the statistical and biological differences in soil bacterial community composition at phylum, class, order, family, and genus levels among different precipitation treatments. We used principal coordinates analysis (PCoA) based on weighted UniFrac distance to assess the impact of altered precipitation on compositional variation of soil bacterial community structure. Significant differences in soil bacterial community structure were analyzed by ANOSIM (analysis of similarities) analysis (Rickbeil et al., 2014).

Network software was used to identify the interactions between bacterial OTUs under different precipitation treatments. To avert spurious correlation, we included only top 50 total abundance of predominant bacterial OTUs in the analysis (Wang et al., 2022). Spearman's correlation analysis was used to reveal the interactions among bacterial OTUs. Spearman's correlation coefficient greater than 0.5 and statistical significance (P<0.05) were defined as robust correlations. Cytoscape v.3.5.0 was used to visualize the network and calculate the network topological properties, such as the number of nodes, the number of edges, and average degree. Each node corresponded to a bacterial OTU. Edge indicated significant correlation between bacterial OTUs. Average degree is the number of edges on a node. Average distance indicates the path length between two nodes.

Spearman's correlation analysis was performed between bacterial community diversity, composition, plant growth characteristics, and soil physical-chemical properties to find the indices that significantly related to soil bacterial community composition and diversity. To analyze the direct and indirect effects of altered precipitation on bacterial community structure, we performed a SEM in Amos v.22.0. Before performing SEM analysis, principal component analysis (PCA) was used to reduce the number of plant growth characteristics and soil physical-chemical properties. All data in SEM were fitted through the maximum likelihood estimation method. On the basis of regression weight estimates, the initial model was simplified by reducing insignificant paths and state variables. The best-fitted model was selected by non-significant χ^2 test, root mean squared error of approximation (RMSEA) index, and goodness-of-fit (GIF) index.

3 Results

3.1 Variation in plant communities and soil properties under altered precipitation

The plant AGB, coverage, density, and height significantly increased with an increase in precipitation (P<0.05, Table 1). Compared with DP20 treatment, IP40 treatment significantly increased AGB. Plant coverage of DP40 treatment was significantly lower than that of IP20 treatment. Compared with CK and increased precipitation treatments, DP40 treatment significantly decreased plant height and density. The plant species richness and Shannon's diversity tended to increase with an increase in precipitation (P>0.05, Table 1).

SWC, MBC, SOC, TN, TP, SAN, and pH maintained unaffected under precipitation treatments (P>0.05), while SAP, SAK, and EC significantly changed along precipitation gradient (P<0.05, Table 1). SAP and EC markedly increased with a decrease in precipitation, and peaked under DP40 treatment. However, SAK under IP40 treatment was significantly higher than that under IP20 treatment (P<0.05, Table 1). In addition, SWC, MBC, and SOC reached the maximum value under IP40 treatment (P>0.05). The value of pH under CK treatment was the highest (P>0.05). However, TN, TP, and SAN peaked under DP40 treatment (P>0.05, Table 1).

3.2 Changes in soil bacterial community structure under altered precipitation

3.2.1 Changes in soil bacterial community diversity

Our results showed that precipitation treatments significantly affected alpha diversity indices of soil bacterial community (Fig. 1a–d). The ACE (abundance-based coverage estimator) index under IP20 treatment was significantly higher than that under DP40 treatment (P<0.05). Compared with CK, precipitation treatments resulted in a significant increase in Shannon's index (P<0.05). However, both decreased precipitation and increased precipitation treatments significantly increased the bacterial Smith-Wilson index compared with CK, and the bacterial Smith-Wilson index was significantly higher under DP40 treatment than those under CK and IP20 treatments (P<0.05).

Table 1 Variations in plant community characteristics and soil physical-chemical properties under different precipitation treatments

Variable	DP40	DP20	CK	IP20	IP40
Species richness	9.3±0.60^{a}	8.5±1.26^{a}	10.2±1.42^{a}	10.0±1.44^{a}	11.3±0.67^{a}
AGB (g/m^2)	84.72±12.31^{ab}	79.24±3.97^{a}	97.10±4.55^{ab}	99.04±15.48^{ab}	127.53±27.11^{b}
Shannon's index	1.65±0.13^{a}	1.27±0.13^{a}	1.59±0.22^{a}	1.38±0.25^{a}	1.71±0.09^{a}
Plant coverage (%)	63.79±12.28^{a}	74.40±6.3^{ab}	82.46±4.69^{ab}	87.58±6.95^{b}	82.37±2.22^{ab}
Plant height (cm)	8.65±0.45^{a}	8.66±0.89^{a}	11.86±0.73^{b}	12.34±0.93^{b}	12.26±0.14^{b}
Plant density (plants/m^2)	82.67±16.6^{a}	139.00±2.02^{b}	161.67±15.88^{b}	144.33±25.18^{b}	163.17±10.31^{b}
SWC (%)	2.87±0.13^{a}	3.21±0.31^{a}	3.56±0.55^{a}	4.08±0.78^{a}	4.41±0.65^{a}
MBC (mg/kg)	354.26±40.94^{a}	349.65±70.47^{a}	375.58±44.1^{a}	371.24±88.95^{a}	378.05±53.55^{a}
SOC (g/kg)	12.54±0.35^{a}	12.24±0.55^{a}	12.72±0.48^{a}	10.86±1.42^{a}	12.95±0.77^{a}
TN (g/kg)	1.87±0.06^{a}	1.65±0.07^{a}	1.78±0.06^{a}	1.57±0.22^{a}	1.80±0.09^{a}
TP (g/kg)	1.36±0.03^{a}	1.32±0.03^{a}	1.33±0.01^{a}	1.31±0.01^{a}	1.33±0.04^{a}
SAN (mg/kg)	86.79±1.59^{a}	79.45±4.89^{a}	86.41±2.33^{a}	76.44±9.42^{a}	85.50±6.22^{a}
SAP (mg/kg）	9.32±0.95^{c}	7.79±0.53^{b}	7.35±1.08^{ab}	5.14±0.55^{a}	5.94±0.53^{ab}
SAK (mg/kg)	191.67±8.82^{ab}	198.33±16.41^{ab}	198.33±6.67^{ab}	170.00±12.58^{a}	208.33±12.02^{b}
pH	8.36±0.04^{a}	8.32±0.12^{a}	8.47±0.04^{a}	8.46±0.05^{a}	8.38±0.03^{a}
EC	314.30±24.48^{b}	243.50±6.14^{a}	236.07±9.4^{a}	207.12±0.86^{a}	218.15±6.86^{a}

Note: AGB, aboveground biomass; SWC, soil water content; MBC, microbial biomass carbon; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; SAN, soil available nitrogen; SAP, soil available phosphorus; SAK, soil available potassium; EC, electrical conductivity. Different lowercase letters within each row indicate significant difference among different precipitation treatments at P<0.05 level. Mean±SD; n=3. DP40, 40% decrease in natural growing season precipitation; DP20, 20% decrease in natural growing season precipitation; CK, control; IP20, 20% increase in natural growing season precipitation; IP40, 40% increase in natural growing season precipitation. The abbreviations are the same in the following figures and tables.

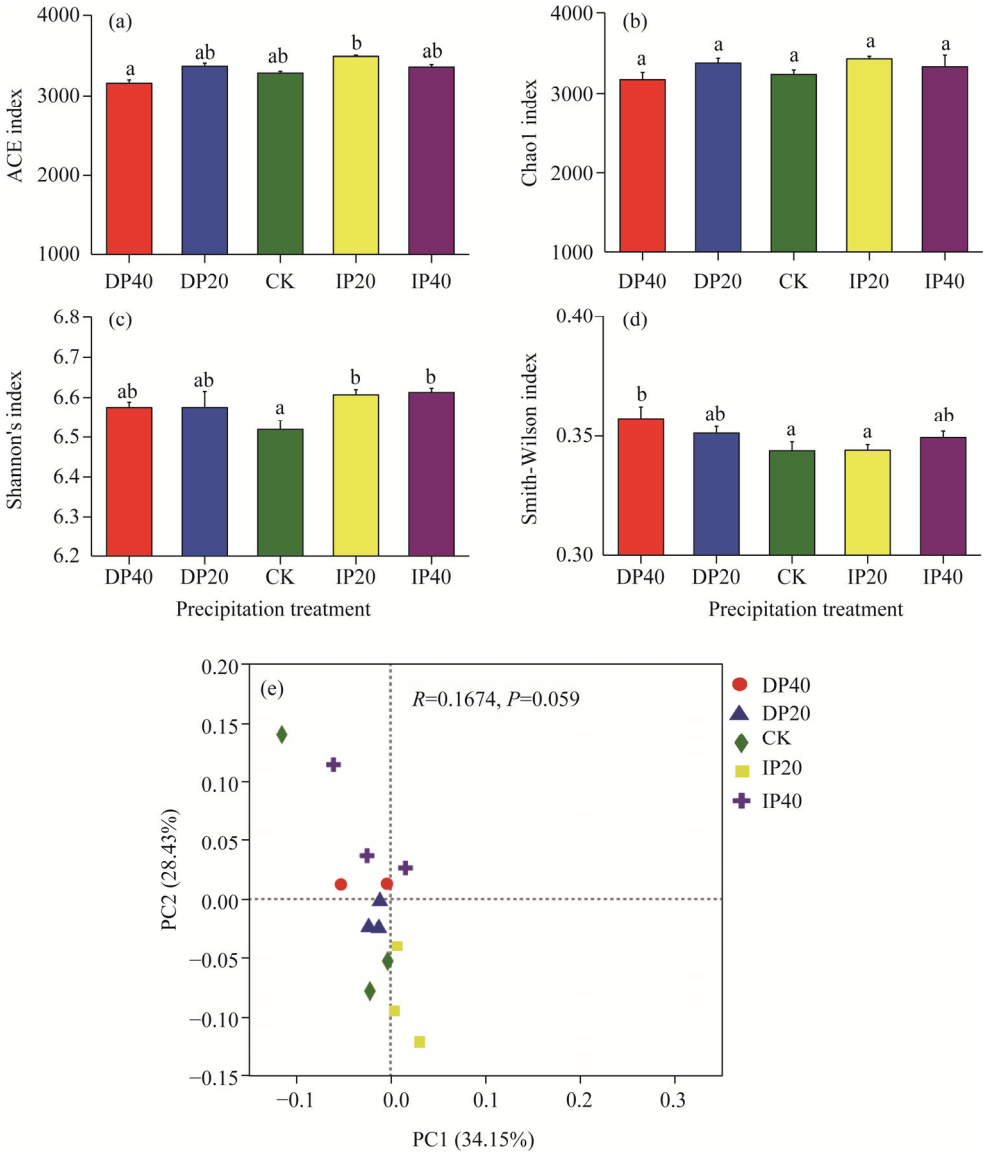

Fig. 1 Changes in alpha diversity indices of soil bacterial community (a–d) and principal coordinates analysis of soil bacterial community composition (e) under different precipitation treatments. Different lowercase letters indicate significant differences among different precipitation treatments at $P<0.05$ level. Bars are standard errors. mACE, abundance-based coverage estimator; PC, principal coordinate.

To assess soil bacterial beta diversity under altered precipitation, we used PCoA to group soil bacterial community. In Figure 1e, the first two axes accounted for 34.15% and 28.43% of the total variance, respectively. However, there was a slightly difference in bacterial communities among precipitation treatments (R^2=0.1674, $0.05<P<0.06$). The first principal coordinate (PC1) interpreted the variance of soil bacterial community between DP20 and IP20, and the second principal coordinate (PC2) interpreted that IP20 was well separated from IP40 and DP40.

3.2.2 Changes in soil bacterial community composition

At the phylum level, soil bacterial community in desert grassland was dominated by Actinobacteria (26.7%–36.0%), Acidobacteria (17.2%–26.1%), Proteobacteria (15.1%–19.3%), and Chloroflexi (12.5%–18.6%), with the total abundance of 83.9% (Fig. 2a). However, there were no significant differences in relative abundance of these phyla among all precipitation treatments ($P>0.10$). Additionally, the abundance of Actinobacteria, Acidobacteria,

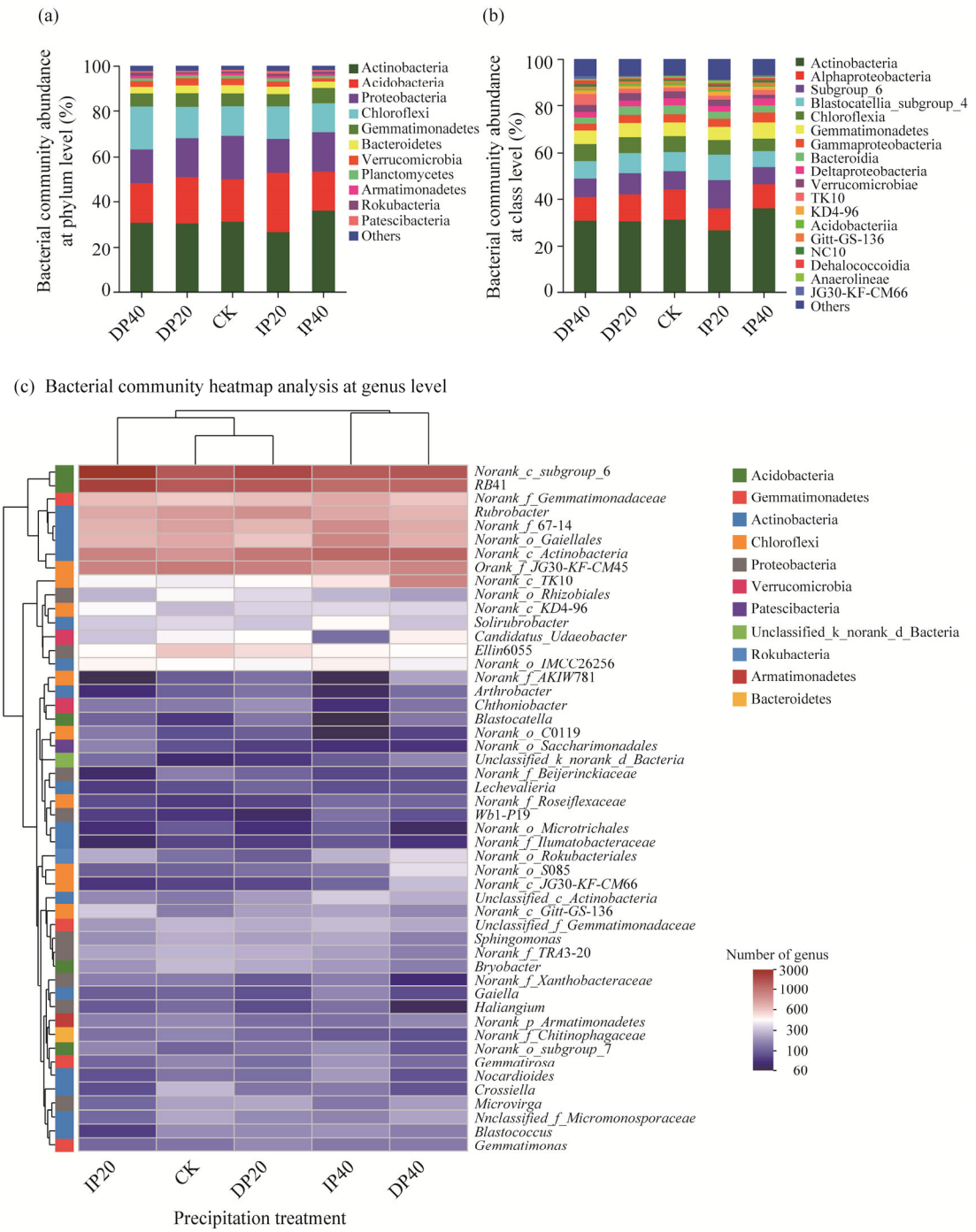

Fig. 2 Bacterial community composition at phylum level (a), class level (b), and genus level (c) under different precipitation treatments

Proteobacteria, and Chloroflexi peaked under IP40, IP20, CK, and DP40 treatments, respectively (Fig. 2a). Meanwhile, there were small differences in the abundance of three phyla (i.e., Acidobacteria, Patescibacteria, and Rokubacteria) along five precipitation gradients ($0.05<P<0.10$).

Totally, 18 dominant soil bacterial classes were screened (average abundance>1%) under precipitation treatments, accounting for 95.8%–96.8% of the total relative abundance (Fig. 2b). Actinobacteria, accounting for 26.7%–36.0% under different precipitation treatments, was the

most abundant class and enriched under IP40 treatment. Furthermore, among bacterial groups with a total abundance greater than 80.0%, 7 of 11 dominant soil bacterial classes were members of Chloroflexi, Proteobacteria, and Acidobacteria phyla. Alphaproteobacteria and Deltaproteobacteria classes were enriched under CK treatment (12.80% and 3.04%, respectively), while Gammaproteobacteria class was enriched under IP40 treatment (4.30%). In Acidobacteria, Blastocatellia_subgroup_4, and subgroup_6 classes were higher under IP20 treatment (12.20% and 11.20%, respectively) than those under other treatments. Furthermore, in the Chloroflexi phylum, Chloroflexia class accounted for 5.30%–7.20%, and was relatively abundant under DP40 treatment, while TK10 class was abundant under IP40 treatment (2.10%).

For a more detailed analysis, a hierarchically clustered heat map was generated to show the hierarchical relationships among the top 50 classified genera under five precipitation treatments (Fig. 2c). The results showed that bacteria genera among CK, DP20, and IP20 and between IP40 and DP40 treatments were most relevant. In general, relative abundance of the top 50 bacterial genus accounted for 74.80%–76.90% of all precipitation treatments. However, relative abundance of most of the genera with significant differences among all precipitation treatments was less than 1.00%, and their highest abundance usually occurred in the precipitation addition treatments (IP20 and IP40). The most representative bacterial genera were *norank_c_subgroup_*6, *RB*41, and *norank_c_Actinobacteria*. Detailed, in Acidobacteria, *norank_c_subgroup_*6 and *RB*41 were abundant under IP20 treatment. *Norank_c_Actinobacteria* belonging to Actindobacteria was abundant under DP40 treatment.

LEfSe method was used to detect soil bacterial populations with significant differences among different precipitation treatments. Totally 23 soil bacterial populations showed statistically striking differences under altered precipitation with LDA scores of >3.0 (Fig. 3). Most differential bacterial groups were significantly enriched under increased precipitation treatments, whereas only 4 bacterial groups were enriched under decreased precipitation treatments (Fig. 3b). After sorting out bacterial groups from phylum to genera according to the LEfSe results, we detected two major response patterns in all samples. The first response pattern was resource-limited populations, such as Thermoanaerobaculia (class), Microtrichales (order), Thermoanaerobaculales (order), Xanthomonadales (order), Nitrosomonadaceae (family), Haliangiaceae (family), Thermoanaerobaculacae (family), *Haliangium* (genus) and *subgroup_*10 (genus), whose relative abundance increased with an increase in precipitation, and were the highest under IP40 treatment (Fig. 3c). In contrast, drought-tolerant populations, including Kallotenuales (order), AKIW781 (family), Hymenobacteraceae (family) and *norank_f_AKIW*781 (genus) had higher relative abundance under decreased precipitation treatments, and were enriched under DP40 treatment (Fig. 3c).

3.2.3 Interaction of soil dominant bacteria under different precipitation treatments

We drew a network graph based on the correlation between bacterial OTUs to reflect the interactions among species in all precipitation treatments. Soil bacterial communities under CK treatment had a more complex network with larger edges (1012) and more average degrees (20.24) than those under reduced and increased precipitation treatments (Fig. 4). Negative interactions among soil bacterial OTUs increased with an increase in precipitation (Table 2). This indicated that drought promoted cooperation among species, while increased precipitation strengthened competition between species. In addition, the average distance of decreased and increased precipitation networks was shorter than that of CK (Table 2). This indicated that altered precipitation shorten the distance between species, resulting in higher capacity to transfer matter, energy, and information between species.

3.3 Driving factors of bacterial community structure under altered precipitation

In the correlation analysis (Table 3), soil bacterial diversity was significantly correlated with precipitation, TN, TP, SAN, SAP, pH, EC, SWC, AGB, Shannon's index and coverage (P<0.05). Soil bacterial alpha diversity (ACE index) was significantly correlated with precipitation, plant coverage, SAP, and EC (P<0.05). The Smith-Wilson index was significantly correlated with

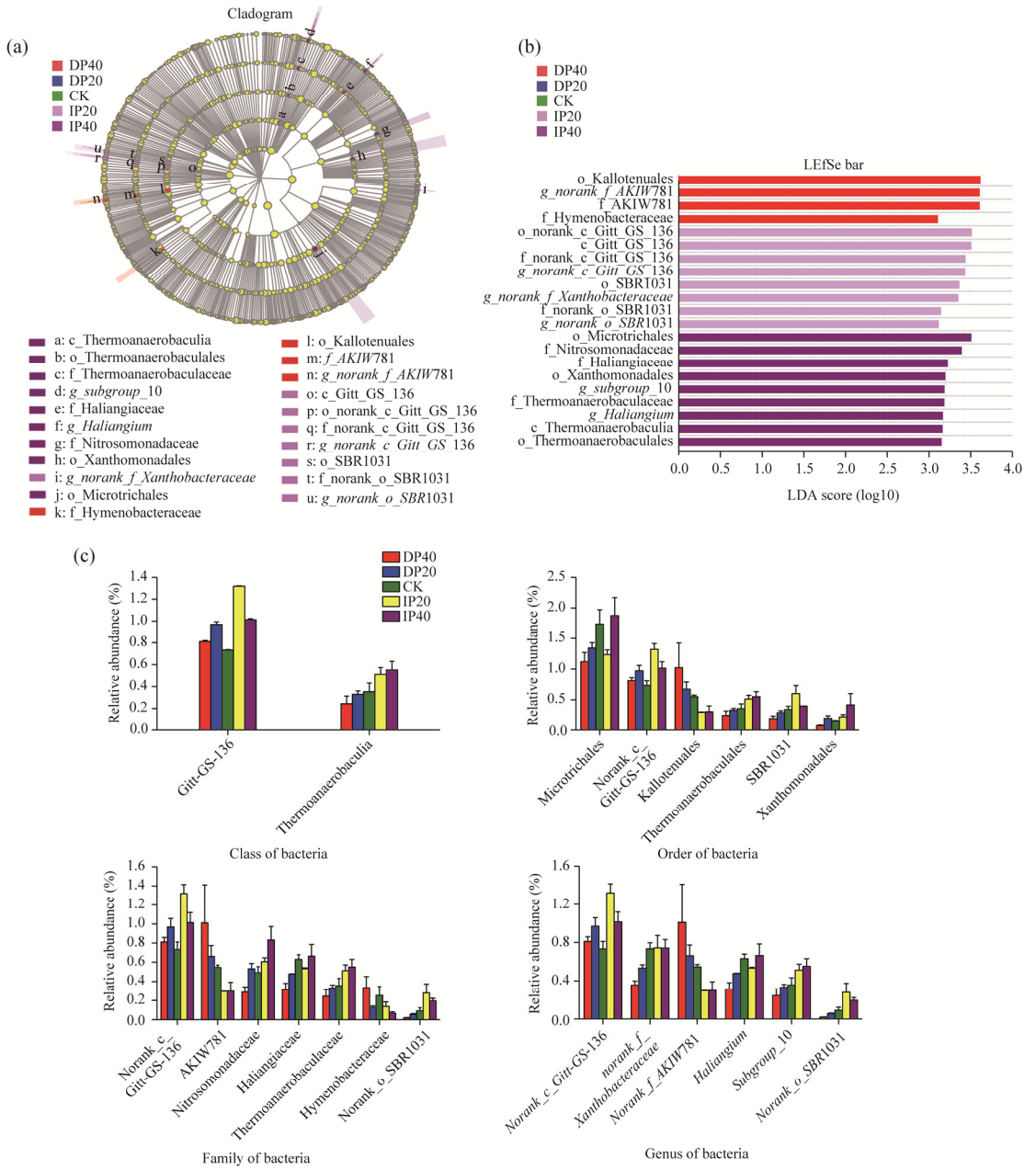

Fig. 3 Result of linear discriminate analysis (LDA) effect size (LEfSe) method of bacterial relative abundance under different precipitation treatments. (a), LEfSe result on bacterial community; (b), histogram of LDA scores computed for differentially abundant bacterial among precipitation treatments identified with a threshold value of >3.0; (c), comparison of relative abundance of bacteria detected by LEfSe analysis from phylum to genus level. Bars are standard errors.

AGB, TN, and pH (P<0.05). Furthermore, the relationship between plant, soil properties, and bacterial beta diversity (PCoA) depended on the chosen weighted or unweighted UniFrac distances (Table 3). In Table 3, precipitation, plant coverage, SAP, EC, and SWC were significantly correlated with unweighted UniFrac distances (P<0.05). Weighted UniFrac distances were significantly correlated with plant Shannon's diversity index, SAN, and TP (P<0.05).

In Spearman's correlation analysis, soil bacterial community composition was significantly related to plant Shannon's index, richness, coverage, and density (P<0.05; Fig. 5). Among them, plant Shannon's index significantly affected seven bacterial phyla (Actinobacteria, Chloroflexi,

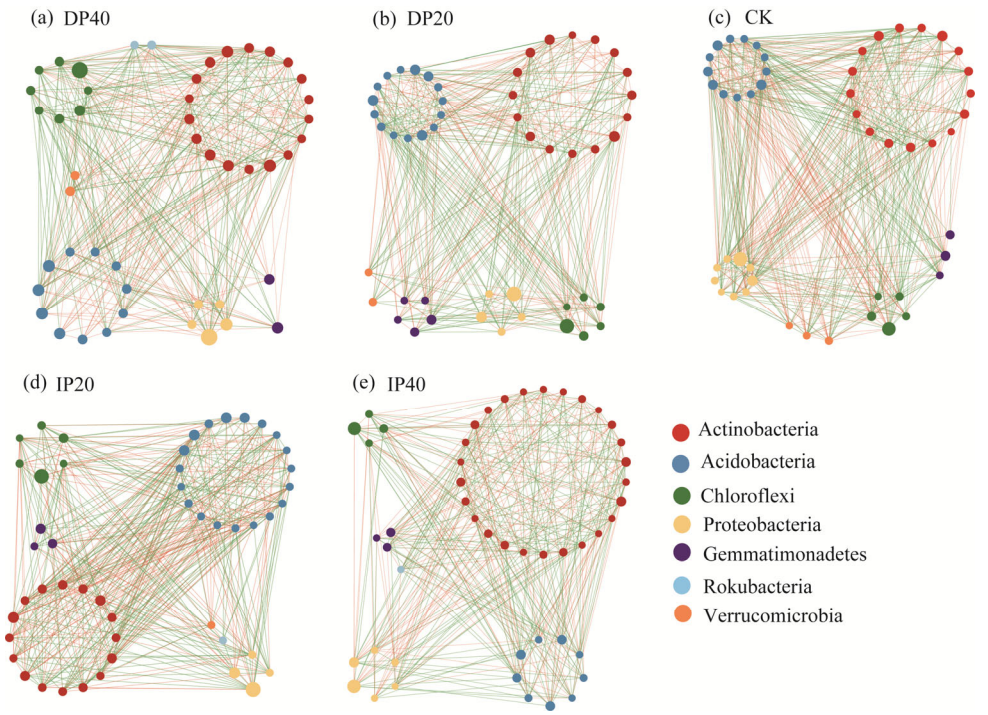

Fig. 4 Interaction among bacterial operational taxonomic units (OTUs) under different precipitation treatments. Red line represents the negative correlation, and green line represents the positive correlation. (a), DP40; (b), DP20; (c), CK; (d), IP20; (e), IP40.

Table 2 Network parameters under different precipitation treatments

Precipitation treatment	Number of nodes	Number of edges	Negative correlation (%)	Average degree	Average distance
DP40	48	782	46.80	16.29	0.35
DP20	49	772	49.87	15.71	0.33
CK	50	1012	49.21	20.24	0.41
IP20	50	834	50.84	16.68	0.34
IP40	49	768	52.60	15.67	0.34

Cyanobacteria, Dependentiae, Fibrobacteres, Gemmatimonadetes, and Patescibacteria), and was the most dominant plant factor. In addition, soil factors that significantly affected soil bacterial community composition at phylum level included SAP, EC, MBC, TN, TP, and SWC (Fig. 5). As the most dominant soil factor, SAP significantly affected five bacterial phyla, such as Acidobacteria, Chlamydiae, Elusimicrobia, Patescibacteria, and WS2. We studied the direct and indirect impacts of altered precipitation on soil bacterial community composition through SEM analysis. The final model well fit our data (x^2=5.864, df=15, P=0.982, RMSEA<0.001), and explained 81% of the variation in plant property, 20% in soil property, and 73% in bacterial community composition (Fig. 6). Altered precipitation significantly changed plant properties, especially plant AGB, which significantly affected soil bacterial community composition (P<0.05). However, altered precipitation did not significantly affect soil properties (P>0.05). Changes in soil factors did not significantly alter plant property and soil bacterial community composition (Fig. 6).

4 Discussion

4.1 Responses of soil bacterial community composition and diversity to altered precipitation

In this study, results indicated that soil bacterial alpha diversity and rare bacterial groups significantly changed with altered precipitation, while bacterial beta diversity and dominant

Table 3 Spearman's correlation coefficients between plant, soil characteristics, and bacterial diversity

Index	Chao1	ACE	Shannon's index	Smith-Wilson index	Unweighted UniFrac distance		Weighted UniFrac distance	
					PCoA1	PCoA2	PCoA1	PCoA2
P	0.453	0.604*	0.437	–0.436	0.818**	0.720**	0.011	–0.131
AGB	–0.100	–0.050	0.057	–0.625*	0.339	0.193	–0.232	–0.507
Species richness	0.013	–0.042	0.307	0.056	0.296	0.424	–0.338	–0.482
Shannon's index	–0.218	–0.257	0.004	0.282	0.186	–0.054	–0.129	–0.675**
Plant coverage	0.254	0.529*	0.036	–0.125	0.486	0.543*	0.271	0.179
Plant height	0.036	0.032	–0.168	0.211	–0.161	0.046	–0.104	–0.107
Plant density	0.050	0.221	0.061	–0.157	0.382	0.418	–0.232	0.118
SOC	–0.164	–0.343	–0.064	0.314	0.132	–0.154	–0.111	–0.450
TN	–0.307	–0.304	–0.271	0.632*	–0.104	0.207	–0.036	–0.507
TP	–0.157	–0.261	–0.154	0.296	0.118	0.057	–0.489	–0.529*
SAN	–0.389	–0.479	–0.354	0.207	0.264	0.064	–0.164	–0.589*
SAP	–0.475	–0.695**	–0.397	0.463	–0.631	–0.549*	–0.490	–0.122
SAK	–0.284	–0.498	–0.311	0.205	0.120	–0.261	–0.253	–0.394
pH	0.039	0.329	–0.068	–0.564*	0.100	0.136	0.043	0.468
EC	–0.349	–0.534*	–0.320	0.411	–0.803**	–0.661**	–0.281	–0.013
SWC	0.039	0.221	0.186	–0.114	0.289	0.550*	0.200	–0.254
MBC	–0.186	–0.111	–0.271	0.489	0.196	0.400	–0.061	–0.275

Note: P, precipitation; AGB, aboveground biomass; SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; SAN, soil available nitrogen; SAP, soil available phosphorus; SAK, soil available potassium; EC, electrical conductivity; SWC, soil water content; MBC, microbial biomass carbon; ACE, abundance-based coverage estimator; PCoA, principal coordinates analysis. *, $P<0.05$ level; **, $P<0.01$ level; ***, $P<0.001$ level.

bacteria groups did not change significantly (Figs. 1 and 3). Soil bacterial communities in the desert grassland were predominated by Actinobacteria, Acidobacteria, Proteobacteria, and Chloroflexi (Fig. 2a). This was consistent with the results in a similar desert grassland (Na et al., 2019) and desert (Wu et al., 2020). In addition, soil low-abundant bacterial groups (relative abundance <1%) rather than dominant bacterial taxa were significantly different among precipitation treatments (Fig. 3). This result suggested that the effects of altered precipitation on soil rare bacterial taxa were stronger than that on dominant bacterial groups, which was consistent with Zhao et al. (2017) and Wu et al. (2020), but was inconsistent with the result in the desert grassland of Inner Mongolia, China (Wang et al., 2021). Methods of altered precipitation might be reasons for the inconsistence. Unlike our field precipitation manipulation experiment, Wang et al. (2021) conducted the experiment along a natural precipitation gradient. Under natural precipitation gradients, there were greater differences in environmental factors, such as precipitation, temperature, evaporation, plant community characteristics, and soil physical-chemical properties (Wang et al., 2021). These changes in environmental factors may further lead to significant differences in soil dominant bacterial abundance along natural precipitation gradients (Wang et al., 2021). In this study, precipitation was not related to weighted UniFrac distance (Table 3). This trend is further confirmed by the low sensitive of dominant species to changes in precipitation, which confirmed by Wu et al. (2011), who found that weighted UniFrac distance placed more emphasis on common taxa. Small precipitation events (less than 10 mm) and long dry period between precipitation events in our study area might be related to this trend (Guo et al., 2021). Therefore, the rapid evaporation of soil water after precipitation event probably weakened the difference in the responses of soil bacterial dominant taxa to precipitation treatments. However, compared with dominant taxa, rare taxa are more susceptible to natural or external disturbances, such as altered precipitation (Shade et al., 2014). A strong correlation

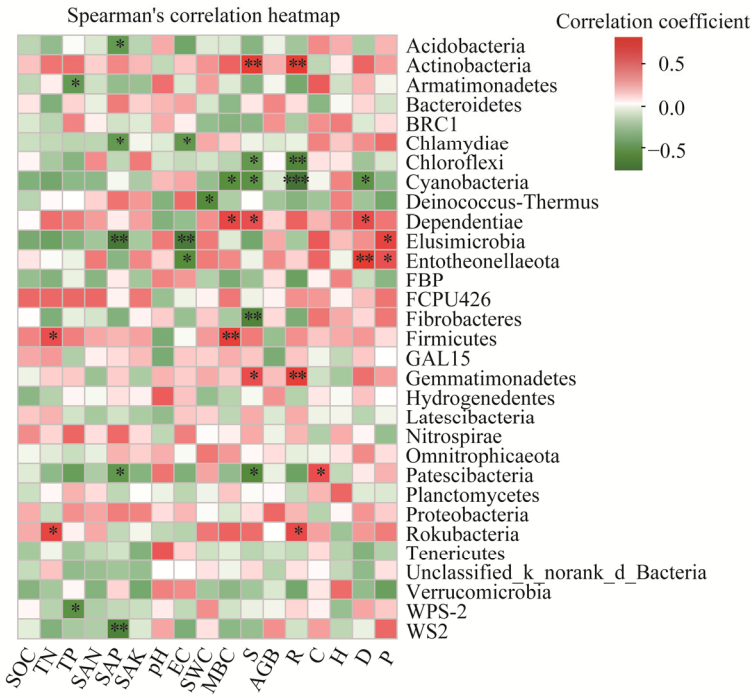

Fig. 5 Relationship of bacterial community composition at phylum level with precipitation, plant, and soil factors. SOC, soil organic carbon; TN, total nitrogen; TP, total phosphorus; SAN, soil available nitrogen; SAP, soil available phosphorus; SAK, soil available potassium; EC, electrical conductivity; SWC, soil water content; MBC, microbial biomass carbon; S, Shannon's index; AGB, aboveground biomass; R, species richness; C, plant coverage; H, plant height; D, plant density; P, Precipitation. *, P<0.05 level; **, P<0.01 level; ***, P<0.001 level.

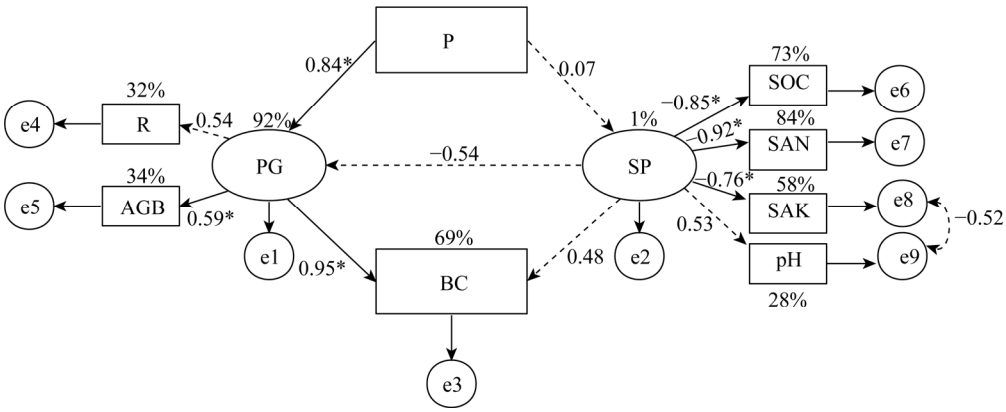

Fig. 6 Structure equation model (SEM) result of the impact of altered precipitation on soil bacterial community. Ellipse represents a potential variable, rectangle represents a measurable variable, and circle represents residual (e1–e9). R, species richness; AGB, aboveground biomass; PG, plant growth; P, precipitation; BC, bacterial community; SP, soil property; SOC, soil organic carbon; SAN, soil available nitrogen; SAK, soil available potassium. *, P<0.05 level.

between precipitation and unweighted UniFrac distance (Table 3) also further confirmed the strong sensitivity of rare taxa to altered precipitation, which was consistent with Wu et al. (2011). Additionally, rare bacterial taxa also provide abundant genetic diversity and functional diversity (Lynch and Neufeld, 2015). Moreover, soil ACE index and Shannon's index increased with an increase in precipitation (Fig. 1), which confirmed the contribution of rare taxa to alpha diversity to some extent, as rare taxa were most abundant in favorable environmental conditions (Shade et

al., 2014; Lynch and Neufeld, 2015).

Furthermore, there were no significant differences in relative abundance of dominant bacterial phyla among precipitation treatments (Figs. 1 and 3), indicating that these bacterial populations could adapt to local climate changes during long-term natural selection (Bouskill et al., 2013). Their adaptability to precipitation fluctuations can lead to greater stability of bacterial community structure under altered precipitation (Meisner et al., 2018). For example, Actinobacteria, Chloroflexi, and Acidobacteria can better tolerate drought or moist by changing the osmotic potential and mediating stress tolerance because of thicker cell walls (Amend et al., 2016). The greater tolerance of these bacterial populations to water stress may further lead to the unchanged bacterial community composition and structure under all precipitation treatments. Anderson et al. (2006) found that variations of soil bacterial beta diversity reflected the similarities or differences in soil bacterial community composition across different precipitation treatments.

4.2 Ecological strategies of soil bacterial populations in response to altered precipitation

LEfSe method at phylum, class, order, family and genus levels showed two patterns of bacterial groups that responded to altered precipitation, i.e., resource-limited populations and drought-tolerant populations (Fig. 3). In this study, resource-limited populations were enriched under IP40 treatment. Most of them belonged to Actinobacteria and Proteobacteria phyla predicted as copiotrophic groups by Fierer et al. (2007). For example, Microtrichales order belonging to the copiotrophic Actinobacteria phylum, was enriched under IP40 treatment (Fig. 3), and the relative abundance of Actinobacteria was positively related to species richness and Shannon's index (Fig. 5). This is because soil nutrients input and nutrient availability increase as plant growth improves under increased precipitation treatments, thereby promoting the growth of resource-limited populations (Manzoni et al., 2014). In contrast, drought-tolerant populations were enriched under DP40 treatment and mostly belonged to Chloroflexi phylum. The Chloroflexi phylum belongs to the drought-tolerant or oligotrophic population (Amend et al., 2016), and the abundance of Chloroflexi was negatively related to species richness and Shannon's index (Fig. 5). Furthermore, given the ability to produce mycelia in some Chloroflexi members (Xian et al., 2020), the growth of certain Chloroflexi members may be improved by decreased precipitation due to promoted hyphal growth and subsequently increased nutrient absorption.

Interaction between bacteria can promote different distribution ratios of bacterial populations under different precipitation treatments (Deng et al., 2012). In this study, IP40 treatment largely promoted competitive relationships among bacteria, while DP40 treatment highly facilitated cooperation among bacteria (Fig. 4), Che et al. (2019) also found that positive and negative interactions among microbial groups. Due to the improved soil water content and nutrient availability under increased precipitation, the activity and growth of bacteria can be enhanced, thereby resulting in stronger competitive interactions among bacterial groups, resulting in resources aggregation (Grime, 1977; Ho et al., 2017). In the network analysis, a negative correlation between Chloroflexi and Actinobacteria phyla indicated the promoted enrichment of Actinobacteria and inhibited growth of Chloroflexi owing to much resource competition under IP40 treatment (Fig. 4). In addition, a positive correlation between Acidobacteria and Chloroflexi in the network analysis indicated the facilitated cooperation in the resource-poor environment under DP40 treatment (Fig. 4). Therefore, the interactions between bacterial taxa under altered precipitation can affect the patterns of bacteria groups.

4.3 Relations among soil bacterial community, vegetation characteristics, and soil environment factors

In this study, we found that altered precipitation can affect soil bacterial community through directly changing plant community (Figs. 5 and 6; Table 3). However, bacterial community was not affected by soil properties (Fig. 6). These results were consistent with existing studies (Mitchell et al., 2010; Koyama et al., 2018), but inconsistent with the result of Na et al. (2019), who found that the effects of altered precipitation on soil properties can indirectly drive the

changes in soil bacterial community composition via regulating plant AGB. In this study, the contribution of plant AGB to the changes in soil bacterial community composition was greater under altered precipitation (Fig. 6). Plant AGB, coverage, height, and density were significantly increased with an increase in precipitation (Table 1). With an increase in precipitation, increasing plant AGB leads to more litter and root secretion (Ren et al., 2015; Liu et al., 2016; Yan et al., 2018), thereby changing soil microbial resource utilization efficiency and the metabolism of soil microorganisms (Delgado-Baquerizo et al., 2013; Lange et al., 2015). Therefore, soil microbial community composition can be affected by the variations of plant AGB under altered precipitation. Furthermore, under altered precipitation, Actinobacteria, Chloroflexi, and Acidobacteria, as soil dominant bacterial phyla and decomposers of recalcitrant carbon substrates, can be directly affected by plant residues characteristics or by the concentrations of secondary metabolites (Bhatti et al., 2017; Janoušková et al., 2018; Liu et al., 2021). These changes in plant residues and secondary metabolites in all precipitation treatments further lead to differences in microbial community composition under altered precipitation. Our previous study found that three-year of extreme drought treatments significantly reduced plant community destiny, height, and coverage by inhibiting seed germination and plant growth, simplified plant community structure, and influenced plant diversity to some extent (Guo et al., 2021). Therefore, the stronger sensitivity of plant community to altered precipitation can further affect soil bacterial communities in desert grassland.

However, soil bacterial community composition was not significantly affected by soil properties under altered precipitation (Fig. 6). This is because field precipitation manipulation experiment only significantly changed EC, SAP, and SAK (Table 1), which makes no difference in soil nutrient (Fig. 6). Therefore, with variations of precipitation, soil bacterial community composition was not shaped by the weak variations of soil properties (Fig. 6). Soil dominant bacterial phyla, Chloroflexi and Acidobacteria phyla belonging to the oligotrophic populations, have the potential to exploit nutrient-poor environments with low energy flows and respond less to changes in soil resource availability caused by altered precipitation (Amend et al., 2016; Ho et al., 2017). Furthermore, with an increase in precipitation, the loss of soil nutrients by runoff and the disruptive effects of soil aggregates by the splashing, collision of raindrops, and the shear forces of runoff may inhibit the growth and reproduction of soil bacteria under increased precipitation treatments (Li et al., 2015; Du et al., 2020; Du et al., 2021). Therefore, with changes in precipitation, soil properties did not contribute to the changes in bacterial community composition in desert grassland.

5 Conclusions

In this study, soil bacterial alpha diversity and rare bacteria significantly changed with altered precipitation, but the dominant bacteria and soil bacterial beta diversity did not change. Increased precipitation promoted species competition. However, decreased precipitation strengthened species cooperation. The response patterns of soil bacterial groups to altered precipitation were resource-limited populations and drought-tolerant populations. SEM analysis showed that altered precipitation can affect soil bacterial community through changing plant community, such as plant AGB. In conclusion, this study showed the possible dynamics and contributors of soil bacterial community diversity and composition under altered precipitation in desert grassland. To accurately assess the trends of soil carbon pools under global climate changes, future studies should focus on analyzing the changes in plant root and its exudates and the relationship between plant root and soil microbial community under altered precipitation.

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References

Amend A S, Martiny A C, Allison S D, et al. 2016. Microbial response to simulated global change is phylogenetically conserved and linked with functional potential. The ISME Journal, 10(1): 109–118.

Anderson M J, Ellingsen K E, McArdle B H. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters, 9(6): 683–693.

Bao S D. 2000. Soil and Agriculture Chemistry Analysis (3rd ed). Beijing: China Agricultural Press, 30–33. (in Chinese)

Bhatti A A, Haq S, Bhat R A. 2017. Actinomycetes benefaction role in soil and plant health. Microb Pathogenesis, 111: 458–467.

Boeddinghaus R S, Marhan S, Berner D, et al. 2019. Plant functional trait shifts explain concurrent changes in the structure and function of grassland soil microbial communities. Journal of Ecology, 107(5): 2197–2210.

Bouskill N J, Lim H C, Borglin S, et al. 2013. Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. The ISME Journal, 7(2): 384–394.

Brookes P C, Landman A, Pruden G, et al. 1985. Chloroform fumigation and the release of soil nitrogen–A rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biology and Biochemistry, 17(6): 837–842.

Caporaso J G, Kuczynski J, Stombaugh J, et al. 2010. QIIME allows analysis of high throughput community sequencing data. Nature Methods, 7(5): 335–336.

Caporaso J G, Lauber C L, Walters W A, et al. 2011. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. Proceedings of the National Academy of Sciences, 108(1): 4516–4522.

Chaudhry V, Rehman A, Mishra A, et al. 2012. Changes in bacterial community structure of agricultural land due to long-term organic and chemical amendments. Microbial Ecology, 64(2): 450–460.

Che R, Wang S, Wang Y, et al. 2019. Total and active soil fungal community profiles were significantly altered by six years of warming but not by grazing. Soil Biology and Biochemistry, 139: 107611, doi: 10.1016/j.soilbio.2019.107611.

Chen H, Zhao X, Lin Q, et al. 2019. Using a combination of PLFA and DNA-based sequencing analyses to detect shifts in the soil microbial community composition after a simulated spring precipitation in a semi-arid grassland in China. Science of the Total Environment, 657: 1237–1245.

Chen Y, Xu T, Veresoglou S D, et al. 2017. Plant diversity represents the prevalent determinant of soil fungal community structure across temperate grasslands in northern China. Soil Biology and Biochemistry, 110: 12–21.

De Deyn G B, Cornelissen J H C, Bardgett R D. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters, 11(5): 516–531.

Delgado-Baquerizo M, Maestre F T, Gallardo A, et al. 2013. Decoupling of soil nutrient cycles as a function of aridity in global drylands. Nature, 502(7473): 672–676.

Deng Y, Jiang Y H, Yang Y, et al. 2012. Molecular ecological network analyses. BMC Bioinformatics, 13: 113, doi: 10.1186/1471-2105-13-113.

Du L, Wang R, Gao X, et al. 2020. Divergent responses of soil bacterial communities in erosion-deposition plots on the Loess Plateau. Geoderma, 358: 113995, doi: 10.1016/j.geoderma.2019.113995.

Du L, Guo S, Gao X, et al. 2021. Divergent responses of soil fungal communities to soil erosion and deposition as evidenced in topsoil and subsoil. Science of the Total Environment, 755: 142616, doi: 10.1016/j.scitotenv.2020.142616.

Edgar R C. 2013. UPARSE: Highly accurate OTU sequences from microbial amplicon reads. Nature Methods, 10(10): 996–998.

Fierer N, Schimel J P. 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biology and Biochemistry, 34(6): 777–787.

Fierer N, Bradford M A, Jackson R B. 2007. Toward an ecological classification of soil bacteria. Ecology, 88(6): 1354–1364.

Grime J P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist, 111(982): 1169–1194.

Guo Y, Zhang L, Zhao R, et al. 2021. Response of plant community characteristics to precipitation change in desert steppe from a monthly-scale perspective. Chinese Journal of Ecology, 40(7): 1895–1906. (in Chinese)

Harris R F. 1981. Effect of water potential on microbial growth and activity. Water Potential Relations in Soil Microbiology, 9: 23–95.

Ho A, Di Lonardo D P, Bodelier P L. 2017. Revisiting life strategy concepts in environmental microbial ecology. FEMS Microbiology Ecology, 93(3): fix006, doi: 10.1093/femsec/fix006.

Huang G, Li L, Su Y, et al. 2018. Differential seasonal effects of water addition and nitrogen fertilization on microbial biomass and diversity in a temperate desert. CATENA, 161: 27–36.

IPCC. 2013. Summary for policymakers. In: Stocker T F, Qin D, Plattner G K, et al. Climate Change 2013: The Physical Science Basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press, 25–45.

Janoušková M, Kohout P, Moradi J, et al. 2018. Microarthropods influence the composition of rhizospheric fungal communities by stimulating specific taxa. Soil Biology and Biochemistry, 122: 120–130.

Jia M, Liu C, Li Y, et al. 2017. Response of fungal composition and diversity to simulated nitrogen deposition and manipulation of precipitation in soils of an Inner Mongolia desert steppe of northern China. Canadian Journal of Soil Science, 97(4): 613–625.

Jordan S E, Palmquist K A, Bradford J B, et al. 2020. Soil water availability shapes species richness in mid-latitude shrub steppe plant communities. Journal of Vegetation Science, 31(4): 646–657.

Knapp A K, Fay P A, Blair J M, et al. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science, 298(5601): 2202–2205.

Koyama A, Steinweg J M, Haddix M L, et al. 2018. Soil bacterial community responses to altered precipitation and temperature regimes in an old field grassland are mediated by plants. FEMS Microbiology Ecology, 94(1): fix156, doi: 10.1093/femsec/fix156.

Kuramae E, Gamper H, Van Veen J V, et al. 2011. Soil and plant factors driving the community of soil-borne microorganisms across chronosequences of secondary succession of chalk grasslands with a neutral pH. FEMS Microbiology Ecology, 77(2): 285–294.

Lange M, Eisenhauer N, Sierra C A, et al. 2015. Plant diversity increases soil microbial activity and soil carbon storage. Nature Communications, 6: 7707, doi: 10.1038/ncomms7707.

Lennon J T, Aanderud Z T, Lehmkuhl B K, et al. 2012. Mapping the niche space of soil microorganisms using taxonomy and traits. Ecology, 93(8): 1867–1879.

Li H, Yang S, Xu Z, et al. 2017. Responses of soil microbial functional genes to global changes are indirectly influenced by aboveground plant biomass variation. Soil Biology and Biochemistry, 104: 18–29.

Li X, Yan Y, Lu X, et al. 2022. Responses of soil bacterial communities to precipitation change in the semi-arid alpine grassland of northern Tibet. Frontiers in Plant Science, 13: 1036369, doi: 10.3389/fpls.2022.1036369.

Li Z, Xiao H, Tang Z, et al. 2015. Microbial responses to erosion-induced soil physico-chemical property changes in the hilly red soil region of southern China. European Journal of Soil Biology, 71: 37–44.

Liu J, Wu N, Wang H, et al. 2016. Nitrogen addition affects chemical compositions of plant tissues, litter and soil organic matter. Ecology, 97(7): 1796–1806.

Liu X, Huang Z, Havrilla C A, et al. 2021. Plant litter crust role in nutrients cycling potentials by bacterial communities in a sandy land ecosystem. Land Degradation & Development, 32(11): 3194–3203.

Lynch M D J, Neufeld J D. 2015. Ecology and exploration of the rare biosphere. Nature Reviews Microbiology, 13(4): 217–229.

Magoč T, Salzberg S L. 2011. FLASH: Fast length adjustment of short reads to improve genome assemblies. Bioinformatics, 27(21): 2957–2963.

Makhalanyane T P, Valverde A, Gunnigle E, et al. 2015. Microbial ecology of hot desert edaphic systems. FEMS Microbiology Reviews, 39(2): 203–221.

Manzoni S, Schimel J P, Porporato A. 2012. Responses of soil microbial communities to water stress: Results from a meta-analysis. Ecology, 93(4): 930–938.

Manzoni S, Schaeffer S M, Katul G, et al. 2014. A theoretical analysis of microbial eco-physiological and diffusion limitations to carbon cycling in drying soils. Soil Biology and Biochemistry, 73: 69–83.

Meier C L, Bowman W D. 2008. Links between plant litter chemistry, species diversity, and below-ground ecosystem function. Proceedings of the National Academy of Sciences, 105(50): 19780–19785.

Meisner A, Jacquiod S, Snoek B L, et al. 2018. Drought legacy effects on the composition of soil fungal and prokaryote communities. Frontiers in Microbiology, 9: 294, doi: 10.3389/fmicb.2018.00294.

Mitchell R J, Hester A J, Campbell C D, et al. 2010. Is vegetation composition or soil chemistry the best predictor of the soil microbial community?. Plant and Soil, 333(1): 417–430.

Na X, Yu H, Wang P, et al. 2019. Vegetation biomass and soil moisture coregulate bacterial community succession under altered precipitation regimes in a desert steppe in northwestern China. Soil Biology and Biochemistry, 136: 107520, doi: 10.1016/j.soilbio.2019.107520.

Ochoa-Hueso R, Collins S L, Delgado-Baquerizo M, et al. 2018. Drought consistently alters the composition of soil fungal and bacterial communities in grasslands from two continents. Global Change Biology, 24(7): 2818–2827.

Preece C, Verbruggen E, Liu L, et al. 2019. Effects of past and current drought on the composition and diversity of soil microbial communities. Soil Biology and Biochemistry, 131: 28–39.

Prein A F, Rasmussen R M, Ikeda K, et al. 2017. The future intensification of hourly precipitation extremes. Nature Climate Change, 7(1): 48–52.

Ren H, Xu Z, Huang J, et al. 2015. Increased precipitation induces a positive plant-soil feedback in a semi-arid grassland. Plant and Soil, 389(1): 211–223.

Rickbeil G J M, Coops N C, Andrew M E, et al. 2014. Assessing conservation regionalization schemes: Employing a beta diversity metric to test the environmental surrogacy approach. Diversity and Distributions, 20(5): 503–514.

Shade A, Jones S E, Caporaso J G, et al. 2014. Conditionally rare taxa disproportionately contribute to temporal changes in microbial diversity. mBio, 5(4): e01371-14, doi: 10.1128/mBio.01371-14.

She W, Bai Y, Zhang Y, et al. 2018. Resource availability drives responses of soil microbial communities to short-term precipitation and nitrogen addition in a desert shrubland. Frontiers in Microbiology, 9: 186, doi: 10.3389/fmicb.2018.00186.

Sorensen P O, Germino M J, Feris K P. 2013. Microbial community responses to 17 years of altered precipitation are seasonally dependent and coupled to co-varying effects of water content on vegetation and soil C. Soil Biology and Biochemistry, 64: 155–163.

Standing D B, Castro J I R, Prosser J I, et al. 2005. Rhizosphere carbon flow: A driver of soil microbial diversity. In: Bardgett R D, Usher M B, Hopkins D W. Biological Diversity and Function in Soils. Cambridge: Cambridge University Press, 57–79.

Umair M, Sun N, Du H, et al. 2020. Bacterial communities are more sensitive to water addition than fungal communities due to higher soil K and Na in a degraded Karst ecosystem of southwestern China. Frontiers in Microbiology, 11: 562546, doi: 10.3389/fmicb.2020.562546.

Wang Q, Garrity G M, Tiedje J M, et al. 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Applied and Environmental Microbiology, 73(16): 5261–5267.

Wang S, Zuo X, Awada T, et al. 2021. Changes of soil bacterial and fungal community structure along a natural aridity gradient in desert grassland ecosystems, Inner Mongolia. CATENA, 205: 105470, doi: 10.1016/j.catena.2021.105470.

Wang Y, Xie Y, Ma H, et al. 2022. Responses of soil microbial communities and networks to precipitation change in a typical steppe ecosystem of the Loess Plateau. Microorganisms, 10(4): 817, doi: 10.3390/microorganisms10040817.

Wu K, Xu W, Yang W. 2020. Effects of precipitation changes on soil bacterial community composition and diversity in the Junggar Desert of Xinjiang, China. PeerJ, 8: e8433, doi: 10.7717/peerj.8433.

Wu Z, Dijkstra P, Koch G W, et al. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. Global Change Biology, 17(2): 927–942.

Xian W, Zhang X, Li W. 2020. Research status and prospect on bacterial phylum Chloroflexi. Acta Microbiologica Sinica, 60(9): 1801–1820. (in Chinese)

Yan J, Wang L, Hu Y, et al. 2018. Plant litter composition selects different soil microbial structures and in turn drives different litter decomposition pattern and soil carbon sequestration capability. Geoderma, 319: 194–203.

Yang X, Zhu K, Loik M E, et al. 2021. Differential responses of soil bacteria and fungi to altered precipitation in a meadow steppe. Geoderma, 384: 114812, doi: 10.1016/j.geoderma.2020.114812.

Zhang L, Xie Z, Zhao R, et al. 2018. Plant, microbial community and soil property responses to an experimental precipitation gradient in a desert grassland. Applied Soil Ecology, 127: 87–95.

Zhang N, Liu W, Yang H, et al. 2013. Soil microbial responses to warming and increased precipitation and their implications for ecosystem C cycling. Oecologia, 173(3): 1125–1142.

Zhang W, Wei H L, Gao H W, et al. 2005. Advances of studies on soil microbial diversity and environmental impact factors. Chinese Journal of Ecology, 24(1): 48–52. (in Chinese)

Zhao Q, Jian S, Nunan N, et al. 2017. Altered precipitation seasonality impacts the dominant fungal but rare bacterial taxa in subtropical forest soils. Biology and Fertility of Soils, 53(2): 231–245.